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# MYLONDON DARWINI OWEN (XENARTHRA, MYLODONTINAE) FROM THE LATE PLEISTOCENE OF MESOPOTAMIA, ARGENTINA, WITH REMARKS ON INDIVIDUAL VARIABILITY, PALEOBIOLOGY, PALEOBIOGEOGRAPHY, AND PALEOENVIRONMENT

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**ABSTRACT**—The subfamily Mylodontinae, typified by *Myodon*, is known from the Colloncuran (late Miocene of Patagonia, Argentina) to the late Pleistocene of South America and North America. Mylodontinae have been recorded during the Pleistocene of Argentina, including the genera *Glossotherium*, *Paraglossotherium*, *Lestodon*, and *Myodon*, with *Paraglossotherium* and *Myodon* not as well known as the other genera. In Argentina there have been traditionally four species of *Myodon*, *M. darwini*, *M. zeballozi*, *M. listai*, and *M. insigne*, although the validity of some has been considered doubtful. A nearly complete skull with an associated mandible of *Myodon darwini* from the late Pleistocene of Mesopotamia, Argentina, is described. The specimen represents the first record of the species in the Mesopotamian region. The morphometric analysis indicates that *M. darwini* had greater individual variability than previously thought. Although based on the results of the morphologic and morphometric analysis, the idea of sexual dimorphism for *M. darwini* is, for the time being, unwarranted. This new record also supports the idea that *Myodon* had great ecological tolerance and was capable of inhabiting climates ranging from cold and arid to warm and humid, and even montane environments.

## INTRODUCTION

Living xenarthrans are distributed almost exclusively in the Neotropical region. They are characterized by a particular skeletal architecture that sets them apart from all other placental mammals. Molecular evidence indicates that they represent one of the four major mammalian clades (Delsuc et al., 2001, 2002; Madsen et al., 2001; Murphy et al., 2001; Moller-Krull et al., 2007; Prasad et al., 2008). Xenarthrans, including fossil species, comprise two clades: Cingulata (armadillos, pampatheres, and glyptodonts), with a bony dermal armor or shield and mainly omnivorous diets, and Pilosa, which includes Vermilingua and Tardigrada. Vermilingua (anteaters) range from terrestrial to arboreal and show marked adaptations to myrmecophagy. Tardigrada (sloths and ground sloths) range from terrestrial to arboreal and are folivorous.

The Tardigrada (sensu Latham and Davies, 1795) or Phyllophaga or Folivora (see further discussion on the use of these terms in Delsuc et al., 2001; Fariña and Vizcaíno, 2003; and McKenna et al., 2006) constitute one of the characteristic mammalian groups for the Cenozoic of South America. The earliest records of the clade correspond to an ungual phalanx and a fragmentary caniniform tooth from the middle Eocene of Antarctica (Vizcaíno and Scillato-Yané, 1995), and a probable record from the late Eocene of Patagonia (Simpson, 1948; McKenna et al., 2006). After the Deseadan (late Oligocene), Tardigrada become abundant in the fossil record, and are represented by several lineages (e.g., Megatheriidae, Nothrotheriidae, Megalonychidae, and Mylodontidae; see Gaudin, 2004; Vizcaíno, 2009) that were especially diversified during the Miocene-Pliocene. Ground sloths of the family Mylodontidae were present in both the Quaternary of South America (e.g., *Glossotherium* Owen, 1839a,

*Lestodon* Gervais, 1855) and North America (e.g., *Paramylodon* Brown, 1903).

The subfamily Mylodontinae, typified by *Myodon* Owen, 1839a, is known from the Colloncuran (late Miocene of Patagonia, Argentina; Scillato-Yané, 1978) to the late Pleistocene of South America and North America. Mylodontinae have been recorded in the Pleistocene of Argentina, including the genera *Glossotherium*, *Paraglossotherium* Esteban, 1993, *Lestodon*, and *Myodon*, with *Paraglossotherium* and *Myodon* not as well known as the other genera (see below).

Chronological and geographically, *Myodon* has been recorded in Argentina (Fig. 1A) from the Ensenadan Stage/Age to the Lujanian Stage/Age (Bargo and Deschamps, 1996; Carlini and Scillato-Yané, 1999; Soibelzon, 2008; Tonni and Carlini, 2008), occurring in many localities of Buenos Aires, Santa Fe, Córdoba, and Santa Cruz provinces (Kraglievich, 1928, 1934; Scillato-Yané, 1976; Bargo and Deschamps, 1996; Carlini and Scillato-Yané, 1999; Tauber and Di Ronco, 2003; Cruz, 2007). The best preserved and known specimen of *Myodon*, a nearly complete skull from the vicinity of the city of Pergamino, Buenos Aires Province, was described by Reinhardt (1879).

Outside Argentina (Fig. 1A), *Myodon* has been recovered from Bolivia (Hoffstetter, 1968; Marshall and Sempere, 1991), Paraguay (Marshall et al., 1984; Carlini and Tonni, 2000), South of Brazil (Oliveira, 1996), Uruguay (Perea and Martínez, 1984; Perea, 1998), and Chile (Alberdi et al., 1987; Borrero et al., 1988; Lopez Mendoza, 2007) (see also Bargo and Deschamps, 1996; Esteban, 1996; Carlini and Scillato-Yané, 1999; Tonni et al., 2003).

The taxonomic history of *Myodon* and the allied genera to which specimens of *Myodon* have been referred (e.g., *Glossotherium*, *Grypotherium* Reinhardt, 1879, and *Neomylodon* Ameghino, 1898) is very complex since the original description of the genus. Several authors (Kraglievich, 1928, 1934; Esteban, 1996; McAfee, 2009) have discussed the nomenclature and systematics of the mentioned genera and contributed to the knowledge of these taxa.

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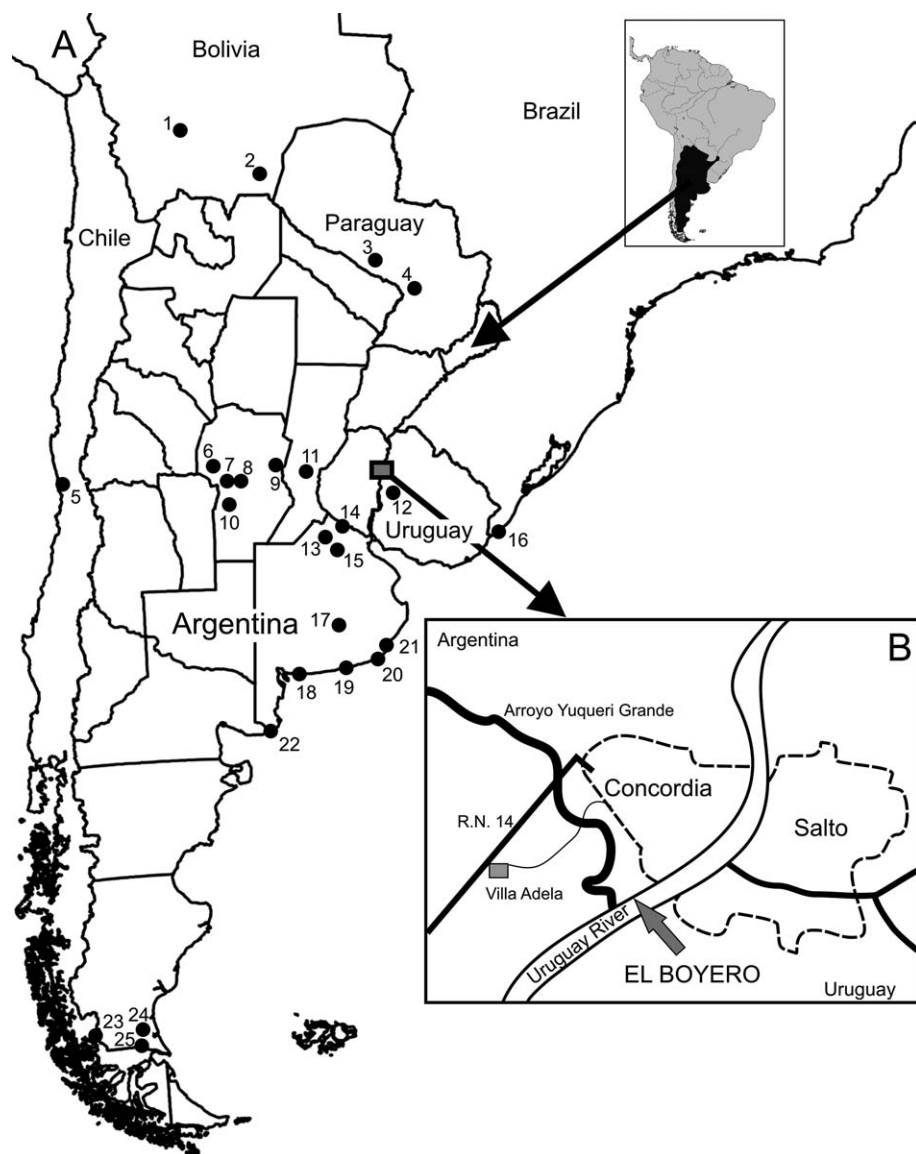


FIGURE 1. **A**, Map of the southernmost part of South America showing the distribution of *Mylodon* during the Quaternary; **B**, detail of the East of Entre Ríos Province, Argentina. 1, Mojotorillo; 2, Ñua Pua; 3, Riacho Negro; 4, General Bruguer; 5, Los Vilos; 6, San Alberto; 7, Calamuchita; 8, Río Tercero; 9, Santa María; 10, Río Cuarto; 11, Carcarañá River; 12, Río Negro Department; 13, Pergamino; 14, San Pedro; 15, Salto; 16, Arroyo Chuí; 17, Olavarria; 18, Punta Alta; 19, Necochea; 20, Miramar; 21, Santa Clara; 22, Carmen de Patagones; 23, Última Esperanza cave; 24, Las Buitreras cave; 25, Fell cave, Cerro Sota, Pali Aike.

In Argentina there have been traditionally four species of *Mylodon*: *M. darwini* Owen, 1839a; *M. zeballozi* H. Gervais and Ameghino, 1880; *M. listai* Ameghino, 1898; and *M. insigne* Kraglievich, 1928 (see Kraglievich 1928, 1934; Esteban, 1996; Carlini and Scillato-Yané, 1999), although the validity of some is considered doubtful (see Kraglievich, 1934; Esteban, 1996; Tonni et al., 2003). Most remains of *M. darwini* from the Pampean region were recovered from sediments referred to the Bonaerian-Lujanian time interval (see Carlini and Scillato-Yané, 1999). *Mylodon listai* was reported from Las Buitreras cave in Santa Cruz Province in sediments referred to the Lujanian Stage/Age (Scillato-Yané, 1976; Alberdi et al., 1987; Carlini and Scillato-Yané, 1999). *Mylodon insigne* was cited with doubts for the Bonaerian-Lujanian interval of the Pampean region (Kraglievich, 1928, 1934; Cione and Tonni, 1999). Kraglievich (1934) considered *M. zeballozi* as a synonym of *M. darwini*. In addition to the specimen described by Reinhardt (1879), other not as well-preserved and incomplete cranial remains of *M. darwini* were described and illustrated by Kraglievich (1928, 1934), Esteban (1996), and Bargo (2001). In sum, the fossil record of

*M. darwini* in Argentina is scarce, and most of the materials are incomplete or not well preserved.

Based on its record, *Mylodon darwini* has been traditionally linked to open areas and temperate to cold semiarid climate (Scillato-Yané et al., 1995; Esteban, 1996). Besides, *M. darwini*, as most of Tardigrada (McDonald 1987, 1995; Naples, 1987, 1989, 1990, 1999), had herbivorous habits and it is one of the few extinct ground sloths for which dung is preserved that provides direct evidence of the plants eaten (see Moore, 1978). Recently, several contributions (Bargo et al., 2006a, 2006b; Vizcaíno et al., 2006; Bargo and Vizcaíno, 2008), based on biomechanics and morpho-functional studies, have reached some hypothesis related to feeding habits of different genera of Tardigrada from the Quaternary of the Pampean region (i.e., *Mylodon*, *Glossotherium*, *Lestodon*, *Scelidotherium* Owen, 1839b, *Megatherium* Cuvier, 1796).

The study of Quaternary vertebrates from the Mesopotamia, Argentina, in particular those referred to the Pleistocene mammals of Entre Ríos Province, has recently experienced an important advance. Many contributions have allowed a better understanding of the fossil record in the area, proposing



FIGURE 2. MACNC Pv 2334, articulated skull of *Mylodon darwini* in lateral view.

biostratigraphic and paleobiogeographic hypotheses (see Carlini et al., 2004; Ferrero, 2005, 2006, 2007, 2008a, 2008b, 2009; Vucetich et al., 2005; Ferrero and Noriega, 2007; Ferrero et al., 2007; Prevosti and Ferrero, 2008; Zurita and Ferrero, 2009; Gasparini and Ferrero, 2010).

Ferrero et al. (2007) reported the first Lujanian mammal assemblage, e.g., *Stegomastodon platensis* (Ameghino, 1888), *Tapirus* cf. *T. terrestris* (Linnaeus, 1758), *M. darwini*, from the El Palmar Formation (late Pleistocene) in the east of Entre Ríos Province (Fig. 1B). Only *S. platensis* had been previously mentioned for that unit (Tonni, 1987). The discovery of a specimen of *M. darwini* in the El Palmar Formation is important because it represents the first record for the species in the Mesopotamian region of Argentina and the skull and associated mandible described here (Fig. 2) are among the better preserved remains of the species.

The aim of this paper is to describe this specimen, compare it with other specimens of *M. darwini*, discuss aspects of individual variability, paleobiology, and paleobiogeography of the species, and discuss paleoenvironmental aspects of the El Palmar Formation.

**Institutional Abbreviations**—BM(NH), Natural History Museum, London, England; MACNC Pv, Colección Paleontología Vertebrados del Museo de Antropología y Ciencias Naturales de Concordia, Concordia, Argentina; MACN Pv, Colección Paleontología Vertebrados del Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMCIPAS, Museo Municipal Centro de Investigaciones Paleontológicas y Arqueológicas de Salto ‘José Fernando Bonaparte,’ Salto, Argentina; MMP M, Colección Paleontología Vertebrados del Museo Municipal de Mar del Plata ‘Lorenzo Scaglia,’ Mar del Plata, Argentina; MNHN-BOL, Museo Nacional de Historia Natural, La Paz, Bolivia; ZMUC CN, Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

## MATERIALS AND METHODS

Skulls and mandibles of *M. darwini* used for comparison are listed in Appendix 1, with indication of geographic and chronological data for each specimen. The biostratigraphic/chronostratigraphic scheme proposed by Cione and Tonni (2005) was followed. Seventeen cranial measurements (Fig. 3A–C) in ten nearly complete skulls and eleven mandibular measurements (Fig. 3D–E) in three nearly complete mandibles were taken. The measurements for the specimens considered are listed in Table 1. Most of the anatomical measurements were defined following Esteban (1996).

**Measurement Abbreviations**—ACW, articular condyle width; AMH, anterior mandibular height; AMW, anterior mandibular internal width; ANH, anterior nasal height; ANW, anterior nasal

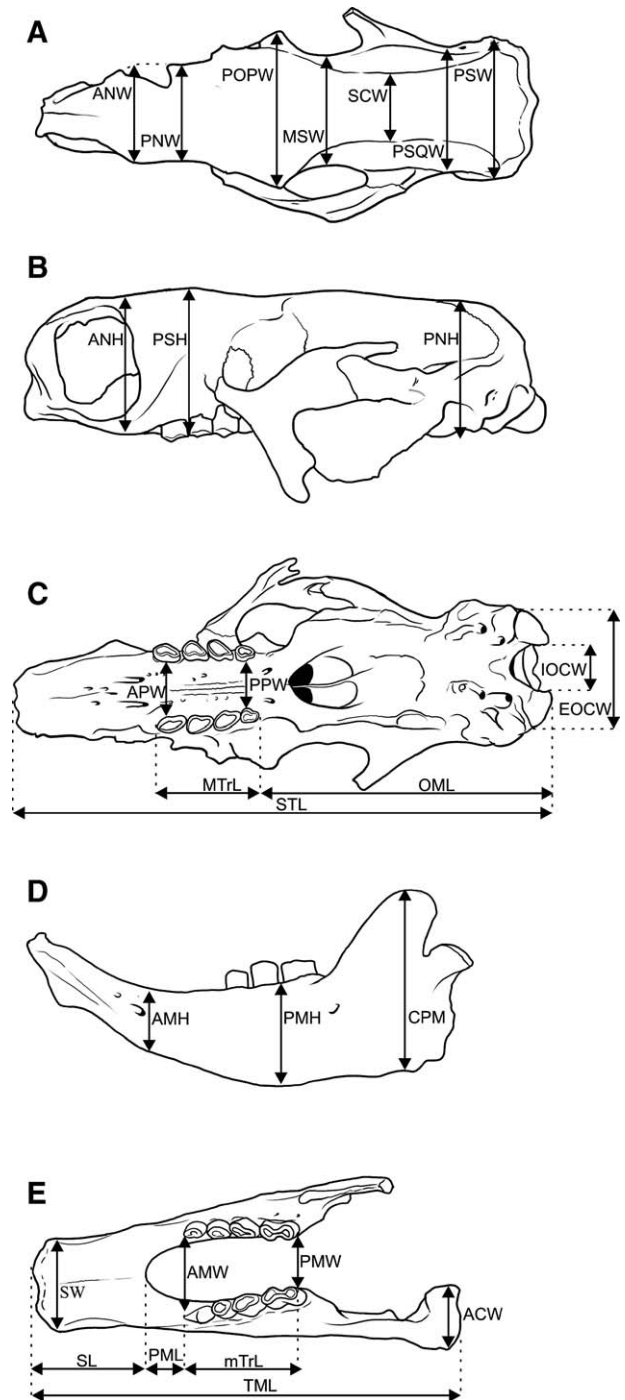


FIGURE 3. Measurements used for comparisons. A–E, *Mylodon darwini* (MACNC Pv 2334). A–B, skull; C–D, mandible. A, dorsal view; B, lateral view; C, palatal view; D, lateral view; E, occlusal view. **Abbreviations:** ACW, articular condyle width; AMH, anterior mandibular height; AMW, anterior mandibular internal width; ANH, anterior nasal height; ANW, anterior nasal width; APW, anterior palate width at the level of M1; CPH, coronoid process height; EOCW, external occipital condyles width; IOCW, internal occipital condyles width; MSW, medium skull width; MTrL, upper molariform tooth-row length; mTrL, lower molariform tooth-row length; OML, distance between the occipital condyles and the posterior edge of M4; PMH, posterolateral mandibular height; PML, premolariform length; PMW, posterior mandibular internal width; PNH, posterior nasal height; PNW, posterior nasal width; POPW, postorbital process width; PPW, posterior palate width at the level of M4; PSH, posterior skull height; PSQW, postsquamosal width; PSW, posterior skull width; SCW, sagittal crest width; SL, symphysis length; STL, skull total length; SW, symphysis width; TML, total mandibular length.

TABLE 1. Measurements (in mm) of skull and mandible of *Myiodon darwini*.

Skull	STL	OML	MTrl	ANW	PNW	MSW	PSQW	PSW	APW	PPW	
MACNC Pv 2334	605	335	109	113	99	115	140	165	66	59	
MLP 3–122	660	365	133	151	140	132	170	197	72	60	
MLP 3–762	—	385	123	131	125	125	160	184	63	48	
MLP 3–763	—	330	126	126	118	121	158	175	55	—	
MLP 3–764	715	365	126	155	123	165	185	225	70	65	
MLP 36-VIII-12-1	—	383	122	—	140	125	155	185	68	53	
MACN 15348	—	—	119	—	—	—	157	175	47	37	
MACN Pv 13882	—	—	120	—	—	—	160	180	80	74	
MMCIPAS B-50–2458	—	320	124	—	128	140	165	180	70	50	
MNHN-BOL-V 006470	590	335	122	118	125	—	—	210	74	64	
Mean value	642.5	352.25	122.4	132.33	124.75	131.85	161.11	187.6	66.5	55.66	
Range of values	590–715	320–383	109–133	113–155	99–140	115–165	140–185	165–210	47–80	37–74	
Skull	IOCW	EOCW	ANH	PNH	PSH	POPW	SCW				
MACNC Pv 2334	51	139	150	155	140	179	75				
MLP 3–122	56	150	180	198	190	180	110				
MLP 3–762	56	160	154	175	165	150	75				
MLP 3–763	58	139	—	—	—	—	—				
MLP 3–764	60	177	235	210	175	210	124				
MLP 36-VIII-12–1	50	148	—	155	170	155	75				
MACN Pv 15348	46	128	—	—	—	—	—				
MACN Pv 13882	—	—	—	185	170	175	95				
MMCIPAS B-50–2458	58	128	—	175	165	180	75				
MNHN-BOL-V 006470	70	170	185	190	160	200	125				
Mean value	56.11	148.77	180.8	180.37	166.87	178.62	94.25				
Range of values	46–70	128–170	150–235	155–198	140–190	150–210	75–125				
Mandible	TML	mTrL	PML	SL	AMH	PMH	CPM	SW	AMW	PMW	ACW
MACNC Pv 2334	440	120	66	110	68	105	195	100	102	75	60
MMP M 4701	420	150	55	140	90	127	—	122	110	100	—
MACN Pv 911	480	125	48	122	65	106	205	—	—	—	45
Mean value	446.66	131.66	56.33	124	74.33	112.66	200	111	106	87.5	52.5
Range of values	420–480	120–150	48–66	110–140	65–90	105–127	195–205	100–122	102–110	75–100	45–60

**Abbreviations:** ACW, articular condyle width; AMH, anterior mandibular height; AMW, anterior mandibular internal width; ANH, anterior nasal height; ANW, anterior nasal width; APW, anterior palate width at the level of M1; CPH, coronoid process height; EOCW, external occipital condyles width; IOCW, internal occipital condyles width; MSW, medium skull width; MTrL, upper molariform tooth row length; mTrL, lower molariform tooth row length; OML, distance between the occipital condyles and the posterior edge of M4; PMH, posterolateral mandibular height; PML, premolariform length; PMW, posterior mandibular internal width; PNH, posterior nasal height; PNW, posterior nasal width; POPW, postorbital process width; PPW, posterior palate width at the level of M4; PSH, posterior skull height; PSQW, postsquamosal width; PSW, posterior skull width; SCW, sagittal crest width; SL, symphysis length; STL, skull total length; SW, symphysis width; TML, total mandibular length.

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A principal components analysis (PCA) was performed from the variance-covariance matrix using INFOSTAT/P 7.1. Only seven specimens (MACNC Pv 2334, MLP 36-VIII-12-1, MLP 3-762, MLP 3-764, MLP 3-122, MMCIPAS B-50-2458, and MNHN-BOL-V 006470) and 14 skull measurements (APW, EOCW, IOCW, MSW, MTrL, OML, PNH, PNW, POPW, PPW, PSH, PSQW, PSW, and SCW) were utilized as a compromise between maximizing the number of specimens and variables that could be included.

#### GEOLOGICAL SETTING

The fossils were found at 'El Boyero' village (31°25'S, 58°02'W), located near the city of Concordia, Entre Ríos

Province, on the coast of the Uruguay River (Ferrero et al., 2007) (Fig. 1B). The material was found in the El Palmar Formation (Iriondo, 1980). This unit is composed of quartz sands and lenses of siliceous pebbles and gravels (chalcedony, opal, and quartz, with subordinated sandstone and basalt fragments) (Iriondo and Kröhling, 2008). The sediment contains significant fine grain-size fraction (silt and clay) and ferric cement, giving the deposits an ochre-colored appearance. Three different facies can be distinguished: (a) fine quartz sands, yellowish and reddish in color, poorly selected, having cross-bedded or planar stratification; (b) clast-supported pebbles and gravels (up to 20 cm) in lens-shaped strata with coarse planar stratification and interbedded medium-coarse sands; (c) silts and clays with high content of iron oxides.

The lithological unit from which the specimen was collected varies in thickness with outcrops from 3 to 12 m thick, and extends 24 m below the subsoil, as corroborated by boreholes. It can be observed from the city of Mocoretá (Corrientes Province) to the city of Concepción del Uruguay (Entre Ríos Province), along 200 km (Iriondo and Kröhling, 2008).

At different localities, the El Palmar Formation overlies Cretaceous basalts and sandstones (Serra Geral and Yeraú formations), the Tertiary Fray Bentos Formation, and the Hernandarias Formation (Pleistocene in age). Otherwise, it underlies the Concordia Formation, which constitutes the Holocene lower terrace of the Uruguay River (Iriondo and Kröhling, 2008).

The present course of the Uruguay River at the middle basin has a fitted meandering pattern, flanked by a continuous

lower terrace formed by the Concordia Formation. The El Palmar Formation constitutes the upper terrace, which appears discontinuously along the river integrating a wide alluvial belt. This terrace is well defined, particularly at the outlet of the tributaries, appearing very eroded by these streams (Iriondo and Kröhlhling, 2007). The main palaeostream that generated this lithological unit can be reconstructed from satellite images. A more wandering pattern than present can be deduced, showing 5–6 km radius of curvature. The western boundary of the alluvial belt is a Pliocene-Quaternary erosion surface named Feliciano-Federal, composed by ancient fluvial and paludal deposits (e.g., Ituzaingó, Salto, San Salvador, and Hernandarias formations) (Iriondo and Kröhlhling, 2008).

Thermoluminescence (TL) data obtained in Entre Ríos Province indicate ages of  $80.7 \pm 13.4$  Ka B.P. (datum from city of Federación) and  $88.4 \pm 35.7$  Ka B.P. (datum from city of Salto) (Iriondo and Kröhlhling, 2007), suggesting a correlation with the OIS 5a.

#### SYSTEMATIC PALEONTOLOGY

TARDIGRADA Latham and Davies in Forster, 1795

MYLODONTIDAE Gill, 1872

MYLODONTINAE Gill, 1872

*MYLODON* Owen, 1839

**Type Species**—*Mylodon darwini* Owen, 1839a.

*MYLODON DARWINI* Owen, 1839a  
(Figs. 2, 4)

**Referred Material**—MACNC Pv 2334, nearly complete skull and mandible (Figs. 2, 4).

**Geographic Provenance**—‘El Boyero’ locality ( $31^{\circ}25'S$ ,  $58^{\circ}02'W$ ), near city of Concordia, Entre Ríos Province, Argentina (Fig. 1B).

**Stratigraphic Provenance**—El Palmar Formation (Iriondo, 1980), early Lujanian (Ferrero, 2009).

#### DESCRIPTION

The following description of *M. darwini* is based mainly on MACNC Pv 2334; additional information is provided on the basis of comparison with other specimens (Appendix 1). MACNC Pv 2334 is nearly complete, without post-mortem deformation, but lacks the right jugal, left m1, right articular condyle of the mandible, and both angular processes (Figs. 2, 4).

**Skull**—In dorsal view (Fig. 4A), the skull is relatively long and wide at the level of the postorbital process and mastoid region. The postorbital processes are more prominent than in other Mylodontinae (e.g., *Lestodon*, *Glossotherium*). In MACNC Pv 2334 the postorbital processes are well developed and projected as pyramidal prominences, whereas in MLP 3–762 these processes are less developed, and in MLP 3–122 are very robust but less projected. The dorsal edge of the temporal fossa is concave both anteriorly and posteriorly, and subparallel in the middle portion (Fig. 4A). As in other Mylodontinae (e.g., *Glossotherium*, *Paramylodon*), the dorsal edges of the temporal fossae are separated and do not form a sagittal crest; in many Megatheriinae (i.e., *Megatherium*, *Eremotherium* Spillmann, 1948), a sagittal crest is present. In MACNC Pv 2334, the mastoid region is wide but not as wide as in other specimens (e.g., MLP 3–122, MLP 3–764, MLP 36-VIII-12-1, MMCIPAS B-50-2458, MNHN-BOL-V 006470; see Table 1). In MACNC Pv 2334, as in most specimens (e.g., MLP 3–122, MLP 3–762, MACN Pv 13882), the rostrum is large and the lateral margins are relatively parallel, whereas in MNHN-BOL-V 006470 the rostrum is anteriorly tapered.

In lateral view (Fig. 4B), the skull roof is nearly flat from the dorsal edge of the occiput to the postorbital region, where it raises gradually, forming a slight convexity. At the preorbital

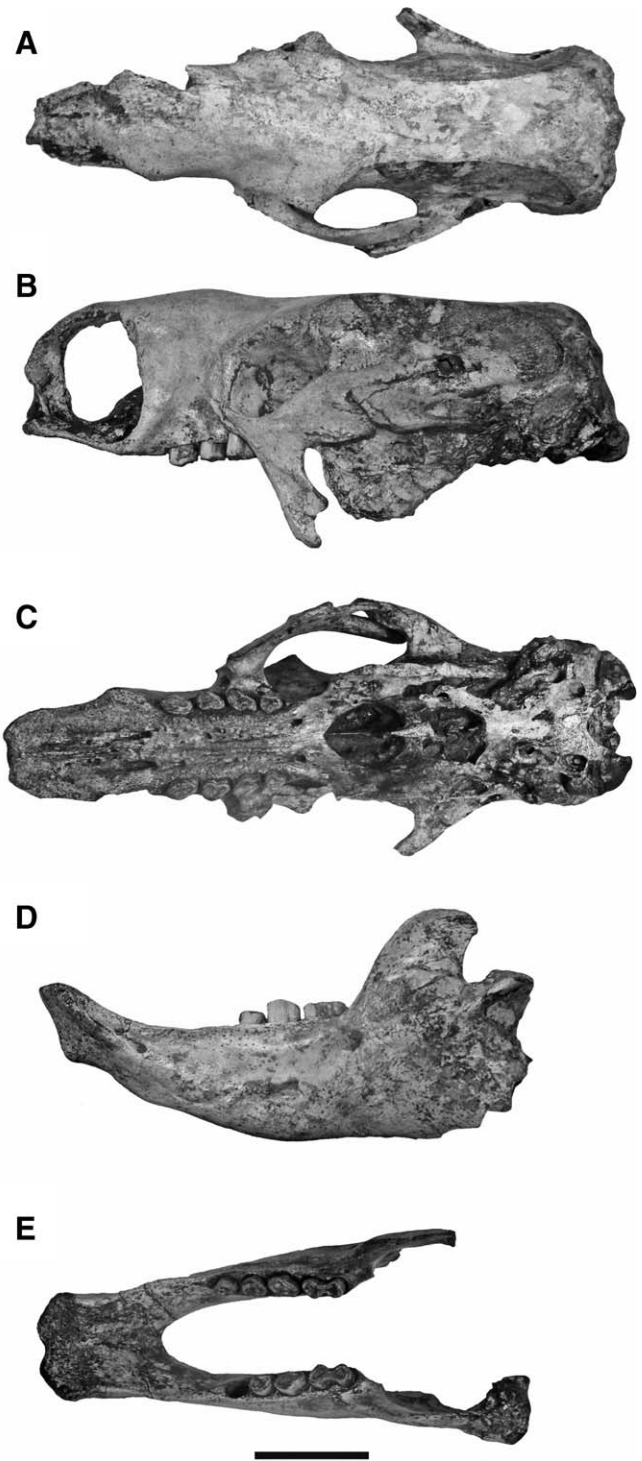


FIGURE 4. *Mylodon darwini* (MACNC Pv 2334), A–B, skull; C–D, mandible. A, dorsal view; B, lateral view; C, palatal view; D, lateral view; E, occlusal view. Scale bar equals 100 mm.

level the profile is somewhat concave and rises at the nasal level. The nasal is very long and extends forward past the anterior margin of the maxilla; additionally, it is convex anteroposteriorly but not as convex as in MLP 3–122, MLP 3–762, MLP 7–64, and MACN Pv 13882, in which it is domed. In MACNC Pv 2334, MACN Pv 13882, MLP 3–122, and MLP 3–762, the highest point

of the skull is located at the level of M1–2, whereas in MLP 3–764 and MNHN-BOL-V 006470 the highest point is anterior to the level of the molariform tooth-row.

As in other specimens of *M. darwini*, the premaxillae have an ascending process that is fused with the nasals and forms a bony arch, which is characteristic of this species (Fig. 4B). This feature was mentioned by Reinhardt (1879) as one of the characteristics for the genus *Grypotherium*.

As in ZMUC CN 43 and MLP 3–764, in MACNC Pv 2334 the anterior part of the ventral edge of the premaxillae rises slightly with respect to the occlusal plane, and the angle that is formed between these portions is greater than in MLP 3–122.

The left jugal is complete (Fig. 4B). The anterior part of its base lies slightly over the level of the occlusal plane and on the plane between the M3 and M4 (Fig. 4B). In MACNC Pv 2334 the ascending process is the longest process and is directed dorsally and posteriorly and, as in MNHN-BOL-V 006470, its dorsal margin is more convex than in ZMUC CN 43. The zygomatic process is the shortest and its posterior margin contacts the jugular process of the squamosal but without fusion. The descending process is slender and is directed ventrally and posteriorly; in MACNC Pv 2334 this process is relatively longer than in ZMUC CN 43. The squamosal forms a subtriangular process that contacts both the ventral margin of the ascending process and the posterior margin of the zygomatic process of the jugal.

The pterygoid is well developed and forms a broad blade-like process between the palatine and the basioccipital region (Fig. 4B). In MACNC Pv 2334, MLP 36-VIII-12-1, and MLP 3–122, the edges of the pterygoid are asymmetric; the posterior margin is longer and less vertical than the anterior, whereas in MLP 3–764 these margins are more symmetric. As in ZMUC CN 43 and MNHN-BOL-V 006470, the ventral edge of the pterygoid does not descend as far ventrally as the plane of the ventral margin of the descending process of the jugal. The lateral surface of the pterygoid has prominent crests for the insertion of the pterygoideus muscle.

The occiput is oblique, forming a 120° angle with the roof of the skull. The ventral edge of the occipital condyles lies at the level of the occlusal plane (Fig. 4B).

In MACNC Pv 2334 the anterior palate is flat, with very prominent rugosities, and many vascular foramina (Fig. 4C), whereas in MLP 3–122 the anterior-most part of the palate is concave labiolingually. In *M. darwini* the premaxillary processes of the maxilla have a V-shaped notch that contacts the medial ramus of the premaxillae; due to the degree of fusion of these elements in MACNC Pv 2334, this notch is not visible. As in other specimens, the molariform tooth rows diverge anteriorly (Fig. 4C; Table 1). The posterior portion of the palate is extended and concave. The postpalatine notch is broad so that the pterygoids are clearly separated. The posterior part of the skull has a similar morphology to that present in other specimens of *M. darwini*, with a large foramen lacerum and condyloid foramen (Patterson et al., 1992; Gaudin, 1995).

The most noticeable feature of the upper dentition of *M. darwini* is the absence of the first tooth that in Mylodontidae is usually termed caniniform (Fig. 4C). The absence of the caniniform is also observed in some specimens of *Paramylodon* (see Brown, 1903; Stock, 1925; McDonald, 1995; McAfee, 2009). In MACNC Pv 2334 the molariform tooth rows are shorter than in other specimens (Table 1). In *M. darwini* the molariforms are simple and rounded, whereas in *Glossotherium*, *Paramylodon*, and *Lestodon* they are more complex. In MACNC Pv 2334 the M1 is oval in cross-section. The M2 is subtriangular in cross-section, with the anterior wall convex and the posterolabially flat. The M3 is subtriangular in cross-section. The M4 is the smallest tooth and is also subtriangular in cross-section.

**Mandible**—The mandible of MACNC Pv 2334 (Fig. 4D–E) presents the usual morphology of other specimens of *M. darwini*

(e.g., BM(NH) M-16617, MACN Pv 991, MMP M 4701, ZMUC CN 43). Compared to other Mylodontinae (e.g., *Lestodon*, *Glossotherium*, *Paramylodon*), in *M. darwini* the horizontal ramus is relatively long, with its greatest depth at the level of the m4, and it decreases gradually in depth toward the mandibular symphysis (Fig. 4D). As in other specimens, the dorsal margin of the mandibular symphysis is above the occlusal plane. Ventrally, the symphysis presents a very developed mental prominence. As in MACN Pv 991 and MMP M 4701, the length of the symphysis is similar to the length of the molariform tooth-row (Fig. 4E). In MACNC Pv 2334, MACN Pv 11502, and BM(NH) M-16617, the space between the posterior margin of the symphysis and the anterior edge of the m1 is relatively greater than in MACN Pv 991 and MMP M 4701 (Table 1). The anterior and lateral margins of the symphysis are slightly concave (Fig. 4E).

The anterior opening of the mandibular canal lies on the lateral wall of the horizontal ramus, slightly posterior to the plane of the posterior margin of the mandibular symphysis (Fig. 4D).

As in other specimens (e.g., ZMUC CN 43, MACN Pv 991), in MACNC Pv 2334, the anterior margin of the coronoid process is posterior to the posterior edge of the m4 (Fig. 4D). The anterior margin of the coronoid process forms a 140° angle with the occlusal plane, whereas the posterior margin lies nearly perpendicular to the occlusal plane. In MACNC Pv 2334, the articular condyle lies over the level of the occlusal plane, whereas in MACN Pv 991 it is below this plane.

The angular process is not completely preserved, but judging by the small portion preserved and the condition observed in other specimens, it lies below the occlusal plane and its posterior margin would have been posterior to the articular condyle.

The posterolateral opening of the mandibular canal is located posterior to the plane of the m4 and below the level of the articular condyle (Fig. 4D).

The molariforms are simple (Fig. 4E) and exhibit a similar morphology to that of other specimens (e.g., BM (NH) M-16617, MACN Pv 991, MACN Pv 11502, MACN Pv 5980). The m1 is oval in cross-section. The m2 is nearly rhomboidal in cross-section and presents a groove on its lingual face. The m3 is rhomboidal in cross-section, with slightly concave edges. The m4 is bilobate with a narrow isthmus. In MMP M 4701, the m1 and m2 are subtrapezoidal in cross-section, and the m3 presents its edges more concave than in MACNC Pv 2334.

**Morphometric Analysis**—The morphometric analysis performed indicates that PC1, PC2, and PC3 explain 90% of total variability (Table 2). MACNC Pv 2334 lies at the lower end of PC1 (Fig. 5).

The first component of the PCA explains the 57.4% of the variance. PC1 would reflect body size because most variables (except OML with a lower weight) load with the same sign and similar loadings (Reyment, 1991; Baxter, 1995). The variables PSQW, PSW, and SCW have the greater weights on PC1. Besides, PNH also has a relatively greater weight on PC1. Thus, MACNC Pv 2334 is opposed to the other specimens being the narrowest and lower than the other specimens. Thus, for PC1, the key differences among the specimens are related to the widths and heights of the posterior portion of the skull.

The second component explains 22.7% of total variance. The variables PNW, PSH, OML, and MTrL have the greater weights with positive sign on PC2. Besides, POPW and PPW have a relative importance for PC2, because their weights are slightly lower and have negative sign. Thus, PC2 is interpreted as a shape vector (Reyment, 1991; Baxter, 1995). The negative sign for POPW shows that in small specimens the postorbital processes are relatively more prominent than in large specimens. Thus, for PC2, the key differences among the specimens are mainly related to width, length, and height of the anterior portion of the skull, shape of the postorbital processes, and the length of the posterior portion of the skull.

TABLE 2. Eigenvalues (and proportion of variance,  $V_x$ ) and loadings for first three principal components for principal components analyses (PCA) based on skull measurements.

PC	Eigenvalue	% of $V_x$	Accumulated% of $V_x$
1	8.03	0.57	0.57
2	3.18	0.23	0.8
3	1.44	0.1	0.9
Loadings variables	PC1	PC2	PC3
PSQW	0.34	0.07	-0.02
PSW	0.34	0.06	0.19
SCW	0.34	-0.08	0.09
MSW	0.32	-0.15	-0.02
PNH	0.32	0.07	0.04
IOCW	0.28	-0.17	-0.1
APW	0.27	-0.09	-0.43
POPW	0.27	-0.31	-0.06
PPW	0.25	-0.25	0.16
EOCW	0.25	0.02	0.56
MTrL	0.22	0.41	-0.22
PSH	0.19	0.44	-0.14
PNW	0.12	0.47	-0.26
OML	-0.02	0.43	0.53

See text and Figure 5 for details.

## DISCUSSION

The systematics of *Myodon* are not yet resolved and the validity of many species is at least doubtful. For the Pleistocene of Argentina, Carlini and Scillato-Yané (1999) listed *M. darwini*, *M. insigne*, and *M. listai*. Scillato-Yané (1976) considered *M. listai* as a valid species based on its smaller size and some anatomical differences in the configuration of the molariforms with respect to *M. darwini*. Esteban (1996, Ph.D. dissertation) proposed that *M. darwini*, *M. listai*, *M. insigne*, and *M. zeballozi* are conspecific, with *M. listai*, *M. insigne*, and *M. zeballozi* as junior synonyms of *M. darwini*. Esteban (1996) considered that *M. listai* is a junior synonym of *M. darwini* because, in addition to the lack of diagnostic features in *M. listai*, the small size of a partial palate referred to that species falls within the range of variability of *M. darwini*. Although a systematic revision is needed to determine the valid species for *Myodon*, it seems probable that *M. darwini* is the only well determined, diagnosed, and valid species of the genus.

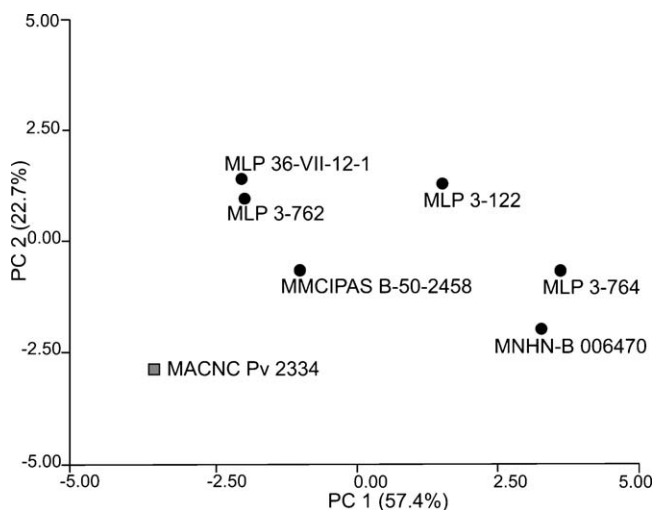


FIGURE 5. Principal components analysis (PCA) of the skulls measurements of *Myodon darwini*. **Abbreviations:** PC, principal component; %, percentage of explained variation.

Cartelle and De Iuliis (2006) examined an ontogenetic series of skulls referred to *Eremotherium laurillardi* (Lund, 1842) (Megatheriidae, Megatheriinae) and determined that the obliteration of the median palatal sutures and transverse palatal sutures (among others) indicates that a specimen had reached maturity. Thus, considering the hypothesis that mylodontids would have had similar ontogenetic stages to those observed in *E. laurillardi* and that most sutures are closed in MACNC Pv 2334, the assignment of the mentioned specimen to an adult individual is justified. In MACNC Pv 2334 the only observable unfused suture occurs between the jugal and the maxilla, a situation common in most skulls of Tardigrada even in the adult stage.

A great degree of individual variability has been proposed for many genera of Tardigrada (see McDonald, 1995; De Iuliis, 1996; Esteban, 1996; White and MacPhee, 2001; Brandoni, 2006; Brandoni et al., 2008, among others). Esteban (1996) considered the range of variability of *M. darwini* to be less than that observed in other Mylodontinae (i.e., *Glossotherium*, *Lestodon*, and *Paraglossotherium*). Taking into account the general morphology of MACNC Pv 2334 (e.g., dental formula, presence of a nasal arch), its assignment to *M. darwini* is justified. The smaller size and some anatomical details present in the El Palmar Formation specimen (e.g., its gracile proportions, lesser convexity of the nasal, location of the articular condyle of the mandible) indicate that a great range of individual variation is also present in *M. darwini*.

The results of the morphometric analysis performed herein indicate that MACNC Pv 2334 falls at the lower end of the size range for *M. darwini*. Moreover, most measurements of MACNC Pv 2334 indicate that this specimen is smaller and narrower than other specimens referred to *M. darwini*, particularly those recorded from the Pampean region of Argentina.

Although the sample from the El Palmar Formation is very small (only one individual) and there are many factors that could be related to the range of individual variability (e.g., genetic, nutritional reasons), we discuss three possible explanations that could be related to the small size of MACNC Pv 2334. One is related to sexual dimorphism, a second is associated with the geological age of the specimen, and a third explanation is linked with paleobiological, paleobiogeographical, and paleoenvironmental aspects.

With regard to sexual dimorphism, studies in living sloths such as *Bradypus torquatus* Illiger, 1811 (see Lara-Ruiz and Chiarello, 2005; Chiarello, 2008) indicate the existence of sexual dimorphism, with females heavier than males. However, the differences in body length are not significant (see Lara-Ruiz and Chiarello, 2005, for the discussion of this topic). In fossil sloths there does not seem to be any unequivocal anatomical features that indicate the presence of sexual dimorphism. Nevertheless, some speculations have been done on the basis of cranial morphology of *E. laurillardi* and *Paramylodon harlani* (Owen, 1839a). For *E. laurillardi*, Cartelle and Bohórquez (1982) and De Iuliis (1996) considered that variation in the temporal region of the skull, which presents two morphologies, could be explained by sexual dimorphism, although the assignment to a specific sex was difficult (De Iuliis, 1996). For *P. harlani*, McDonald (1995, 2006) mentioned the presence of two skull morphs (robust and gracile) and that the differences in size and morphology of the caniniforms could be related to sexual dimorphism. The results of the morphometric analysis herein performed for *Myodon*, which only includes seven specimens, do not demonstrate two clearly separated morphologies that should be considered as males and females. MACNC Pv 2334 is smaller and more slender than other specimens of the species herein studied, but the assignment of MACNC Pv 2334 to a specific sex seems to be unreasonable based on the available specimens and data.

A second alternative to explain the smaller size of the El Palmar Formation specimen could be associated with the geological age of the specimen and the evolution of the clade. For many



Tardigrada it has been postulated that during the phylogeny of a specific lineage there was an increase in body size through time, so each succeeding species was on the average larger than the preceding species (see McDonald, 1995; Esteban, 1996; McDonald and Pelikan, 2006). As was mentioned, the assemblage from the El Palmar Formation is referred to the early Lujanian ( $80.7 \pm 13.4$  ka B.P.; Iriondo and Kröhling, 2007, 2008; Ferrero, 2009) but unfortunately there is no accurate stratigraphic provenance (and absolute age) for most cranial remains herein considered, so this hypothesis cannot yet be tested for *M. darwini*. Tauber and Di Ronco (2003) indicated that a specimen of *M. darwini* was reported from Santa María Department, Córdoba Province, from sediments that were dated to be about  $26.0 \pm 0.5$  ka. B.P. Tonni et al. (2003) reported dates for *Myiodon* sp. from Última Esperanza cave (also named Cueva de Milodón), southern Chile, between  $13.6 \pm 0.2$  ka. B.P. and  $10.2 \pm 0.4$  ka. B.P. Taking into account the available information, it would be possible that most specimens of *M. darwini* from the Pampean region probably come from the uppermost part of the Lujanian and not from the Bonaerian; but new records with better stratigraphic control are needed to establish a correct stratigraphic distribution of the species.

Finally, there are some physical and biological factors that determine the geographic distribution of the species (Cox and Moore, 2000). The identification of these limiting factors is often difficult for extant species and might be even more so for extinct ones. However, some reasonable inferences on paleobiology could be done on the basis of the geographic and stratigraphic distribution of a species, and the paleoenvironmental context.

Studies performed on phytoliths and wood assemblages from the El Palmar Formation (Zucol et al., 2005) provide some information on the paleoenvironment and climate of this unit. The fossil wood assemblage indicates the presence of a mixed forest and palm community. The mixed forest (mainly Anacardiaceae and Mimosoideae) grew on non-swampy soils in temperate-warm and humid-subhumid climatic conditions (Zucol et al., 2005). The presence of palms, which are characteristic elements of subtropical-tropical flora, further indicates a temperate-warm and humid climate (see Brea, 1994, 1998, 1999; Brea and Zucol, 2001). Besides *M. darwini*, Ferrero et al. (2007) identified from the El Palmar Formation the presence of *S. platensis*, *Morenelaphus* cf. *M. lujanensis* (Ameghino, 1888), *Antifer* sp. Ameghino, 1889, *Toxodon* cf. *T. platensis* Owen, 1837, *Macrauchenia patagonica* Owen, 1838, *Tapirus* cf. *T. terrestris*, *Equus neogeus* Lund, 1840, and *M. americanum* Cuvier, 1796. These taxa, excluding *Tapirus* cf. *T. terrestris*, are present in the Lujanian Stage/Age of the Pampean region and were associated with open grassland areas, with more arid and colder climate than that present today (Tonni et al., 1999; Tonni, 2007). *Tapirus terrestris* is usually found in rainforest, subtropical forest, and subtropical savannah, mostly associated with permanent rivers and lagoons, in warm and humid climate.

The facies association and the paleogeomorphology clearly indicate a fluvial environment. This involves sand and conglomerate facies, which constitute bedforms and channel accretion macroforms, and fine-grained sediments accumulated on floodplains. The high-flow dynamics interpreted from the coarsest clast-supported deposits allows an inference of high water discharge, produced by a humid hydrological regime. Otherwise, the high content of iron, resulting from secondary mobilization, reinforces the inference of dominant humid conditions. Moreover in Brazil, at present, it has been observed that secondary hematite ( $\text{Fe}^{+3}$ ) forms where the mean annual temperature is above  $17^\circ\text{C}$ , mean annual precipitation exceeds mean annual evapotranspiration by 900 mm or more, and the soil organic matter is less than 3% (Kämpf and Schwertmann, 1983). Chronologically, the El Palmar Formation ( $80 \pm 13$  Ka B.P.; Iriondo and Kröhling, 2007, 2008) corresponds to OIS 5a (last interglacial), suggesting that

deposition occurred in the early Lujanian (Ferrero, 2009), under warm and humid conditions (Opdyke, 1995; Shackleton, 1995). Thus, taking into account the paleobotanical records, mammal assemblage, sedimentary characterization, and age of the El Palmar Formation, the deposition of the formation occurred in warm and humid climate conditions. The inferred paleoenvironment is interpreted as a closed or forested environment in association with open areas, and the presence of rivers and lagoons related to the Uruguay River and its tributaries.

These warm conditions may have contributed to the smaller body size of *M. darwini* in this region given the proposed a correlation between small body size and warm conditions (e.g., Bergmann's 'rule'; see Bergmann, 1847). In this context, many researchers have speculated on the factors that are involved in the geographic distribution of fossil sloths of North America (see Akersten and McDonald, 1991; McDonald et al., 2000; McDonald et al., 2004; McDonald and Pelikan, 2006). McDonald et al. (2004) indicated a positive Bergmann's response for *P. harlani* from the late Pleistocene of North America, with the average size of the species increasing with an increasing of latitude (and cold conditions). However, the consistency of Bergmann's 'rule' is controversial and there is no agreement among authors on its validity (see Geist, 1987; Meiri and Dayan, 2003; Blackburn and Hawkins, 2004; Brehen and Fiedler, 2004; Meiri et al., 2007; Rodriguez et al., 2008). Again, in the case of *M. darwini*, the sample is too small and it is not easy to test size trends against latitude.

Several contributions, based on the geographic and stratigraphic distribution of *Myiodon*, have indicated that this genus inhabited cold and arid to semiarid climates (see Moore, 1978; Scillato-Yané et al., 1995; Esteban, 1996). The presence of *M. darwini* in interglacial periods (e.g., El Palmar Formation, Arroyo Chuí, South of Brazil) (see Oliveira et al., 2005; Ribeiro et al., 2007; Ferrero, 2009) and in glacial periods (as those registered for the Lujanian Stage/Age of the Pampean region and Patagonia) would indicate that this species was associated with different types of paleoenvironment. This evidence suggests that *Myiodon* had a great ecological tolerance.

Traditionally *Myiodon* was considered a grazer in open areas (Moore, 1978; Scillato-Yané et al., 1995). The paleoenvironmental interpretations related to the geographic and stratigraphic distribution of the genus and the kind of vegetation (i.e., Cyperaceae, Gramineae) that were found in the dung of *Myiodon* that comes from Última Esperanza cave (Moore, 1978) contribute to this interpretation of the species' feeding adaptation. On the other hand, recent studies based on biomechanics and functional morphology (Bargo et al., 2006a, 2006b; Bargo and Vizcaíno, 2008) indicate that *M. darwini* is a mixed or selective-feeder capable to select specific plants or parts of plants. Thus, taking into account the plant assemblage from the El Palmar Formation and the actual feeding specializations considered for *M. darwini*, this species would have had a broad range of suitable vegetation to select as food.

Finally, as was mentioned, many materials collected from the late Lujanian Stage/Age of Patagonia, Argentina (e.g., Las Buitreras cave, Santa Cruz Province) and Chile (e.g., Última Esperanza cave) have been referred to *Myiodon* sp., *M. darwini*, or *M. listai* (based on its smaller size). One specimen referred to *Myiodon* is significant to mention, MACN Pv 19003 was collected in Las Buitreras cave and corresponds to a juvenile individual, as the epiphyses of the tibia are unfused with the diaphysis. The total length of the tibia (290 mm) is greater than those of many tibia of *M. darwini* collected in the Pampean region (see Kraglievich, 1934). Therefore, not all the specimens recovered from the late Lujanian Stage/Age of Patagonia are smaller than those from the Pampean region. Independent of the systematic arrangement (i.e., validity or not of *M. listai*), the presence of some small specimens of *Myiodon* at high latitudes of South America could be due

to their mountainous habitat, because such areas generally support smaller-sized species (Pujos, 2008; Rodríguez et al., 2008).

### SUMMARY

The specimen of *M. darwini* herein described represents the first record of the species in the Mesopotamia region of Argentina. The morphometric analysis indicates that *M. darwini* had greater individual variability than previously thought. Although based on the results of the morphologic and morphometric analyses, the idea of sexual dimorphism for *M. darwini* is, for the time being, unwarranted. This new record also supports the idea that *Myiodon* had a great ecological tolerance, capable of inhabiting arid to semiarid and cold climate, warm and humid climate, and even cold and montane environments.

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- APPENDIX 1.** List of specimens studied with geographic and stratigraphic provenance.
- BM(NH) M-16617, holotype of *M. darwini*, mandible with molariforms. Punta Alta, near Bahía Blanca, Buenos Aires Province, Argentina. Late Pleistocene.
- MACN Pv 991, right dentary with molariforms. Salado River, Buenos Aires Province, Argentina. Pleistocene.
- MACN Pv 11502, incomplete left dentary, lacking m2 and m4, angular process, coronoid process, articular condyle, and symphysis. Carcaraña River, Santa Fe Province, Argentina. Pleistocene.
- MACN Pv 5980, incomplete left dentary lacking m1 and m2, angular process, coronoid process, articular condyle, and symphysis. Pleistocene.
- MACN Pv 15348, restored skull. Buenos Aires Province, Argentina. Pleistocene.
- MACN Pv 13882, incomplete skull lacking prementary region, zygomatic arches, and most molariforms. City of Necochea, Buenos Aires Province, Argentina. Pleistocene.
- MLP 3–122, incomplete skull lacking jugals and molariforms. Buenos Aires Province, Argentina. Pleistocene.
- MLP 3–762, incomplete skull of a non-adult individual, lacking prementary region, molariforms, and jugals. City of Olavarría, Buenos Aires Province, Argentina. Pleistocene.
- MLP 3–763, incomplete skull lacking jugals and molariforms. City of Olavarría, Buenos Aires Province, Argentina. Pleistocene.
- MLP 3–764, nearly complete skull lacking part of the nasal arch. City of Olavarría, Buenos Aires Province, Argentina. Pleistocene.
- MLP 36-VIII-12–1, incomplete skull lacking prementary region, jugals, and molariforms. Bunge station, Buenos Aires Province, Argentina. Pleistocene.
- MMCIPAS B-50–2458, incomplete skull lacking zygomatic arch, and part of nasals. City of Salto, Buenos Aires Province, Argentina. Late Pleistocene.
- MMP M 4701, nearly complete mandible lacking right and left angular process, right and left coronoid process, and right and left articular condyles. Santa Clara, Buenos Aires Province, Argentina. Lujanian (late Pleistocene–early Holocene).
- MNHN-BOL-V 006470, nearly complete skull lacking right jugal and molariforms. Near Mojotorillo, Potosí Department, Bolivia. Pleistocene.
- ZMUC CN 43, nearly complete skull with mandible. Near city of Pergamino, Buenos Aires Province, Argentina. Pleistocene.